

A Set of Discrete Formulae for the Performance of a Tsetse Population During Aerial Spraying

S. J. Childs

Department of Mathematics and Applied Mathematics, University of the Free State,

P.O. Box 339, Bloemfontein, 9300, South Africa.

Tel: +27 51 4013386 Email: simonjohnchilds@gmail.com

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Abstract

A set of discrete formulae that calculates the hypothetical impact of aerial spraying on a tsetse population is derived and the work is thought to be novel. Both the original population and the subsequent generations which survive the aerial spraying, may ultimately be thought of as deriving from two, distinct sources. These origins are, however, neither distinct, nor relevant by the third generation. It is for this reason that the female population is considered to be composed of the following four categories for the purposes of derivation: Original flies which existed as such at the commencement of spraying; original pupae which existed as such at the commencement of spraying; the immediate descendants of both the aforementioned categories, during spraying; third and higher generation descendants. In theory, the latter category is a recurrence relation. In practice, the third generation's pupal stage has hardly come into existence, even by the end of a completed operation. Implicit in the formulae is the assumption of one, temperature-dependent mortality rate for the entire pupal stage, a second for the period between eclosion and ovulation and yet a third for the entire, adult life-span. Gravid female resistance to the insecticide is assumed to be inconsequential. A further assumption of the formulae is that at least one male is always available (degree of sterility variable).

Keywords: Tsetse; *Glossina*; aerial spraying; trypanosomiasis; nagana; sleeping sickness.

1 Introduction

The *Glossina* genus is the vector of trypanosomiasis in Africa. There are about thirty three species and subspecies of tsetse fly, whereas about half as many trypanosomes of the salivarian

clade are thought to exist (Gooding and Krafur, 2004; Stevens and Brisse, 2004). Thirty six African countries are still afflicted by human, African trypanosomiasis (HAT), although nagana is still of veterinary and economic importance in others e.g. South Africa (Anonymous, 2012).

The most common causes of nagana in livestock are *Trypanosoma congolense* and *T. vivax*, in that order of priority. Neither pathogen has ever been known to infect a human host, although both domestic and wild animals serve as the reservoir for the human afflictions, *T. brucei gambiense* and *T. brucei rhodesiense*. *T. gambiense* is associated with chronic disease in West Africa, while *T. rhodesiense* is associated with acute disease in East Africa. Although the advance of HAT is spectacularly rapid in the case of *T. rhodesiense*, *T. gambiense* can be dangerously insidious, the symptoms often only becoming manifest once it is too late to treat (95% of all HAT cases are attributed to *T. gambiense* according to Anonymous, 2012). Not enough is known about the vector competence of the various tsetse species, as was recently illustrated by the findings of Motloang et al. (2009). The *fusca* and *palpalis* groups are largely confined to West Africa, while the *morsitans* group is largely confined to the Eastern side of the continent, a few exceptions to this rule occurring in both the *fusca* and *morsitans* groups. Three members of the *morsitans* group, namely *Glossina morsitans*, *Glossina pallidipes* and *Glossina austeni* could be considered to be mainly problematic in the Southern and East African theatres, while the problem assumes a far greater diversity around Lake Victoria and to the west of it. Members of the *palpalis* group are notorious vectors in the West African theatre (*Glossina fuscipes fuscipes*, in particular, having been implicated by the focus of numerous epidemics).

Trypanosomiasis is regarded by many African countries to be largely of veterinary and economic importance, in modern times. This has certainly not always been the case and Leak (1999) provides a grim reminder that in the opening years of the twentieth century, around 200 000 people died of trypanosomiasis in the provinces of Buganda and Busoga alone and that these provinces eventually had to be evacuated. Fèvre et al. (2004) put the figure closer to around two thirds of the lake-shore population, for a slightly longer period and the epidemic reached similar proportions in the Congo river basin (Anonymous, 2012). Today HAT has all but vanished, largely as a result of the all-out war waged against tsetse during the twentieth century. So great has been the success that, in 2010, only 7139 new cases were reported, the biggest contributor being the Democratic Republic of the Congo (Anonymous, 2012).

This is no small achievement and such success has not come without a price. Du Toit (1954) put the cost of *G. pallidipes* eradication from KwaZulu-Natal, in the first half of the twentieth century, at well in excess of £100 000. Properly planned aerial spraying has proved to be the most effective means of tsetse control and it is with the prohibitive costs in mind that this research attempts to make operations as efficient and successful as possible. The modern operation conventionally utilizes a relatively harmless pyrethroid such as endosulfan or deltamethrin (Allsopp, 1984). An aerosol of insecticide is discharged from a formation of aircraft, flying at low altitude (less than 100 metres a.g.l.) and guided by G.P.S. Adult flies are extremely susceptible to the insecticide and kill rates very close to 100% can be anticipated under favourable conditions.

The main challenge to controlling tsetse by aerial spraying is that the pupal stage is largely protected from insecticides. Repeat spray cycles therefore need to be scheduled to kill new

flies which begin emerging immediately after spraying. Both economic and environmental considerations dictate that the number of such cycles be minimised. The problem, however, is that if the time between spray cycles is too long, recently eclosed flies will themselves mature, become reproductive and larviposit. The underlying philosophy to the aerial spraying of tsetse relies heavily on the fact that all developmental periods in the *Glossina* genus are entirely temperature dependent and are therefore readily predictable. By knowing the mean temperature spray cycles can be scheduled two days short of the time to the production of the first larva; the two-day safety margin being designed to ensure that there is no variance in time-to-first-larva to levels below the length of the spray cycle.

The strategy explored in Childs (2011) was one in which the repeated spray cycles are continued until two sprays subsequent to the eclosion of the last, pre-spray-larviposited, female pupae. None of the observations in that work are, however, valid in the event that the operation is terminated one, or more, sprays short and there could be many reasons for pursuing such a strategy in the modern scenario. Costs, environmental considerations and an area-wide, integrated approach to pest management which contemplates the use of the sterile insect technique (Barclay and Vreysen, 2010), are only a few of the reasons why a curtailed operation has increasingly been entertained as a 'knock-down', rather than as an agent of eradication, in recent times. A recent shift in interest from savannah, to the more inaccessible, riverine and forested habitats, in combination with a better understanding of odour-baited targets, pour-ons and dips (Childs, 2010 and Esterhuizen et al. 2006), has led to these alternative counter measures recently having been assigned a far more significant role in control and eradication, than in the past. In the event that spray cycles are not continued for the full duration, the formula derived in Childs (2011) is not appropriate. A more comprehensive set of formulae is required, one which, for example, also accounts for other categories of pupae, such as the immediate, pupal descendents of pre-spray-existing flies, as well as actual flies themselves.

The effect of temperature on aerial spraying, through the reproductive cycle and general population dynamics of the tsetse fly, can easily be taken into account. The same cannot, however, be said for the effect of temperature on spray efficacy, it being a property unique to each and every environment and the conditions prevailing at the time. Very high kill rates usually (though not always) come about as a result of the sinking air associated with cooler weather. It favours the settling of insecticidal droplets. The inherent toxicity of deltamethrin and many other pyrethroids also decreases with temperature, contrary to the toxicity of most insecticides. The effects of anabatic winds, the protection afforded by the forest canopy and multifarious other variables, are just as relevant to spray efficacy. No account is taken of the mechanism in gravid females, whereby lipophilic toxins are excreted, sacrificing larvae in utero for survival, either. The effect of temperature and age on spray efficacy is therefore not modelled and it is, instead, a variable in the formulation. Spray efficacy is usually measured in the field, with hindsight, rather than predicted. Three kill rates of around 99%, 99.9% and 99.99% respectively are entertained in this work. They should be thought of as being broadly associated with the warmer, intermediate and cooler parts of the low-temperature range respectively. It is in this way that the hypothetical impact of aerial spraying on tsetse fly populations is formulated.

The formulae derived in this work are largely a predictive tool. They provide a convenient means of calculating theoretical levels of control in the aerial spraying of tsetse, by way of

spreadsheets and simple algorithms, in which the outcome is based on mean temperature and spray efficacy. They also provide a convenient means of making ‘back-of-an-envelope’ estimates based on first order terms. The formulae provide a means to calculating the outcome at mean temperature. The data presented in Hargrove (1990), for example, suggest that the temperature in tsetse environments often varies little. The restriction to mean temperature is not problematic from a point of view of prediction, since one can usually only forecast mean temperature. An algorithm is the next logical step, brought about by the introduction of variable temperature.

2 Aerial Spraying and the Life-Cycle of the Tsetse Fly

The female tsetse fly mates only once in her life with the chance η that she is successfully inseminated (η is usually taken to be unity). She also produces only one larva at a time. The time between female eclosion and the production of the first larva is known as time-to-first-larva, τ_1 . Thereafter she produces pupae at a shorter interlarval period, τ_2 . The effect of temperature on the first and subsequent interlarval periods has been estimated in the field, using *G. pallidipes*. The predicted mean time taken from female eclosion to the production of the first pupa is obtained using Jackson’s (Anonymous, 1955) temperature-dependent formula,

$$\tau_i = \frac{1}{k_1 + k_2(T - 24)} \quad i = 1, 2,$$

in which $k_1 = 0.061$ and $k_2 = 0.0020$ (Hargrove, 1994 and 1995). The subsequent interlarval periods are predicted using $k_1 = 0.1046$ and $k_2 = 0.0052$ (Hargrove, 1994 and 1995). The interlarval periods are therefore entirely temperature dependent and readily predictable. Use of this formula needs, however, to be tempered by a knowledge of the large standard deviation presented in Hargrove (1994 and 1995), as well as the fact that larviposition usually takes place in the late afternoon, for *G. morsitans* (Potts, 1933, reported by Jackson, 1949, and Brady, 1972), or afternoon shade in the case of *G. palpalis* (Jackson, 1949, and Buxton, 1955). There exists an ever present risk in interpreting the output to have a precision any better than the daily cohort and a discrete model may be more appropriate than a continuous one under these circumstances.

What is the relevance of the above formula? Since the pupae present in the ground are unaffected by insecticide, the idea is to schedule follow-up operations shortly before the first flies to eclose, after spraying, themselves mature and become reproductive. Subsequent sprays are consequently scheduled two days short of the time to the first larva. This length of the spray interval is denoted σ in the formulae to follow. For temperatures of 22 °C and below, both Jackson’s curve and the data reported in Hargrove (2004) suggest that spraying two days before the time to first larva (the one predicted using the Hargrove, 1994 and 1995, coefficients) is sufficient to ensure that none of the recently eclosed female flies ever give birth prior to being sprayed. This observation is supported by the success of operations such as those of Kgori et al (2006). Caution may, however, need to be exercised in the case of *G. austeni*, in that both periods could be shorter than the above formula predicts. This suspicion is based on the small

size of the fly and in keeping with its shorter puparial duration (Parker, 2008). A shorter time between eclosion and the production of the first larva is a concern for the aerial spraying of *G. austeni*. For *G. brevipalpis* one suspects longer periods based on diametrically opposite arguments. The only relevance to aerial spraying in this latter case is economic, inefficiency being the only expected consequence.

Pupae that are successfully larviposited remain in the ground for a period of time. The duration of the period between larviposition and the emergence of the first imago is known as the puparial duration and is denoted τ_0 in this work. The puparial duration is also a function of temperature and may be predicted using the formula

$$\tau_0 = \frac{1 + e^{a+bT}}{k}$$

(Phelps and Burrows, 1969). For females, $k = 0.057 \pm 0.001$, $a = 5.5 \pm 0.2$ and $b = -0.25 \pm 0.01$ (Hargrove, 2004). The fact that pupae usually eclose in the evening (Vale et. al. 1976) again begs the question of over-interpreting precision. There exists an ever present risk in interpreting the output to have a precision greater than the daily cohort and a discrete model is again indicated as being more appropriate than a continuous one.

What is the relevance of the above formula? A cautious strategy advocates that spray cycles should be repeated until after the last pre-spray-larviposited pupae eclose and it is safer to continue until at least two sprays after their eclosion due to variation in the environment. If, under such circumstances, s denotes the total number of sprays, the total duration of the entire spraying operation is $s - 1$ cycles. Again, caution needs to be exercised in that Parker (2008) reports that *G. brevipalpis* takes a little longer than the above formula predicts, whereas the puparial durations of all other species are thought to lie within 10% of the value predicted. For the same conditions which produce a *G. morsitans* puparial duration of 30 days, *G. brevipalpis* has a puparial duration of 35 days. This has important implications for the aerial spraying of *G. brevipalpis*. The shortest puparial duration is that of *G. austeni*. *G. austeni*'s puparial duration was 28 days under the aforementioned conditions. These observations are noteworthy given the South African context of a sympatric, *G. brevipalpis*-*G. austeni* population.

Other aspects of tsetse population dynamics are also largely temperature-dependent (Hargrove, 2004), although soil-humidity can play an as, or more, important role in early mortality, depending on the species (Childs, 2009). While the effects of both temperature and humidity on pupal mortality are known to be important, they vary profoundly according to the exact stage of development and are cumulative, rather than instantaneous. One might therefore surmise that the age-dependence which characterises post-pupal mortality (observed by Hargrove, 1990 and 1993) is largely a consequence of pupal history. Fortunately, variables such as soil-humidity and vegetation index have little to do with metabolic rate, hence the timing of spray cycles, and worst-case values might therefore be used. Alternatively, they can be regarded to vary (and therefore be relevant) only in the medium to long term. In many regions, the level of humidity and temperature are sometimes linked. Pupae are therefore taken to die off at some temperature-dependent, daily rate, δ_0 , and those flies which subsequently emerge have a probability γ of being female. Some comfort can be taken from the knowledge that the effects of natural mortalities are very small in comparison to those due to aerial spraying. They

have little bearing on the overriding trends and, to a certain extent, this knowledge permits a primitive approach. The question of pupal mortality can also be substantially avoided through the use of a steady-state eclosion rate, β . Hargrove (2004) suggests adult mortality to be predictable, almost entirely temperature-dependent, and a knowledge of post-eclosion mortalities infers the eclosion rate and vice versa, assuming the population to be in equilibrium. It is with this wisdom in mind that the derivation will commence.

During the first few hours subsequent to eclosion, the young, teneral fly's exoskeleton is soft and pliable, its fluid and fat reserves are at their lowest and a first blood meal is imperative for its survival. It is at this time that the insect is at its most vulnerable and it is also at this time that its behaviour is least risk averse (Vale, 1974). Post-pupal survival can be defined as $e^{-\delta_1}$ per day for the period between female eclosion and ovulation. Thereafter the female tsetse fly's chances of survival are higher and can be defined as $e^{-\delta_2}$ per day.

The accumulated mortality described above can be modelled linearly as

$$\delta(t, T) = \begin{cases} \delta_0 t & t < \tau_0 \\ \delta_1 (t - \tau_0) + \delta_0 \tau_0 & \text{for } \tau_0 \leq t < \tau_1 - \tau_2 + \tau_0 \\ \delta_2 [t - (\tau_1 - \tau_2) - \tau_0] + \delta_1 (\tau_1 - \tau_2) + \delta_0 \tau_0 & t \geq \tau_1 - \tau_2 + \tau_0, \end{cases}$$

where t denotes age, for the present. For the purposes of later brevity, it is convenient to define a second cumulative mortality, one which commences at eclosion. If t denotes the time elapsed since eclosion, then

$$\delta^*(t, T) = \begin{cases} \delta_1 t & t < \tau_1 - \tau_2 \\ \delta_2 [t - (\tau_1 - \tau_2)] + \delta_1 (\tau_1 - \tau_2) & \text{for } t \geq \tau_1 - \tau_2, \end{cases}$$

is the aforementioned mortality desired. Some actual values of the various mortalities, their associated temperatures and the justification for their selection can be found in Childs (2011).

The spray-survival rate will, in contrast, be assumed to be independent of age, whereas, in actual fact, a mechanism in gravid females exists whereby lipophilic toxins are excreted, sacrificing larvae in utero for the mother fly's own survival. The older the fly, the more developed this mechanism is usually found to be. The dependence of spray efficacy on age has been ignored for two reasons. Firstly, one might reason that a simple trade-off exists between a fly living and a larva dying and further pregnancies should similarly terminate in spontaneous abortion. Secondly, the spray-survival rate is a small number. Whatever the exact value of ϕ may be for these older flies, the value of ϕ^s , or similar, should ensure that such cohorts are decimated by the end of the operation. Of course, ignoring gravid female resistance to the insecticide may result in slightly altered eclosion rates and the use of inappropriate natural mortalities. Some comfort can be taken from the knowledge that the effects of natural mortalities are very small in comparison to those due to aerial spraying. They have little bearing on the outcome.

3 Strategy for Derivation

The emphasis in the derivation is on the female population, since the male tsetse fly's role in reproduction is relatively insignificant. At least one male is always assumed to be available and

any level of sterilization is accounted for by way of a probability of insemination.

A strong case obviously exists for taking the time of the first spray to be zero, rounding the outputs of the aforementioned formulae to the nearest integer cohort and, consequently, developing a discrete model, one in which spraying occurs subsequent to both larviposition and eclosion on days when spraying is relevant. Just some of the factors which recommend such an approach are that eclosion occurs in the afternoon or early evening when the challenges of dehydration are lower, that larviposition usually occurs not very long before that, or coincides with it, that aerial spraying is best carried out at night when low temperatures favour the settling of insecticidal droplets, the daily character of most traditionally available data and unexplained variance.

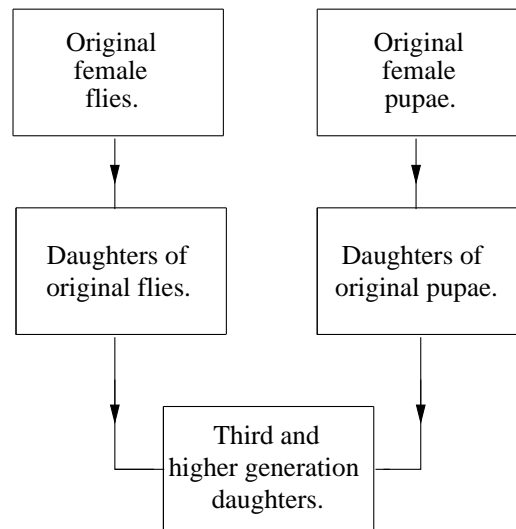
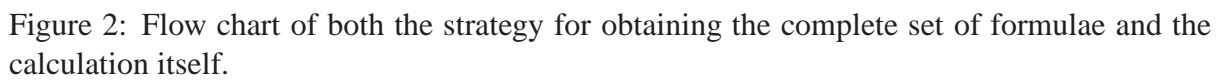


Figure 1: The tsetse population is deconstructed into logically natural categories for the purposes of formulation.

Both the original population and the subsequent generations which survive the spraying, may be thought of as ultimately deriving from two distinct sources (refer to Fig. 1). These origins are, however, neither distinct, nor relevant by the third generation. To understand why this is so, cognizance should be taken of the fact that the number of flies in a given cohort depends on the number of mothers which survived long enough to successfully larviposit, not just on the cohort's own chances of survival since larviposition. There are two distinctly different ancestral origins for the second generation, since mothers existed as either a pupa, or a fly at the commencement of spraying. The same is not true for third generation cohorts since the only generalisation that can be made is that all mothers simply eclosed sometime, subsequent to one puparial duration into the operation, and happened to larviposit on the same day.

symbol	unit	description
N	♀	original, steady-state, equilibrium number of females
η	-	probability of insemination
β	flies $\text{♀}^{-1} \text{ day}^{-1}$	eclosion rate
γ	♀ flies^{-1}	sex ratio
δ_0	day^{-1}	pupal mortality
δ_1	day^{-1}	post-pupal, pre-ovulatory mortality
δ_2	day^{-1}	adult mortality
τ_0	days	pupal duration
τ_1	days	time between eclosion and first larva
τ_2	days	interlarval period
σ	days	length of a spray cycle
s	sprays	total number of sprays
ϕ	-	probability of surviving a single spray
\check{t}	days	time to eclosion since first spray
$E_{\text{pre-spray}}(\check{t})$	flies	time- \check{t} -eclosing cohort which existed as pupae at the commencement of spraying
$E_a(\check{t})$	flies	time- \check{t} -eclosing cohort, larviposited by original, adult females during spraying (second generation)
$E_{ps}(\check{t})$	flies	time- \check{t} -eclosing cohort, larviposited by original, female pupae which existed as such at the commencement of spraying (second generation)
$E_{is}(\check{t})$	flies	time- \check{t} -eclosing cohort, immediately descended from inter-spray-deposited, female pupae (third generation and higher)

Table 1: Symbols used and the quantities they denote.



The observation of two initially distinct origins is, in some sense, an artefact of having separate, ‘start-up’ pupal and fly populations, something which was rendered possible by the assumption

of an equilibrium. Yet the existence of that equilibrium prior to spraying is no artefact.

For the reason that there are originally two distinct sources, it is expedient to deconstruct the surviving population into the following, categories, in the derivation:

1. Original, female flies which existed as such at the commencement of spraying.
2. Original, female pupae which existed as such at the commencement of spraying.
3. Daughters larviposited after the commencement of spraying, including:
 - (a) Daughters of 1 above.
 - (b) Daughters of 2 above.
 - (c) Third generation and higher daughters of this self-same category, 3 above.

Fig. 2 summarises the strategy for both formulation and calculation.

4 Surviving Flies

The actual flies themselves, as distinct from pupae, which survive the last spray are usually of no real consequence to the outcome of spraying (Childs, 2011). This is not necessarily the case in instances in which the operation has been curtailed, or kill rates are low. The state of the adult fly population during spraying is, nonetheless, what ultimately determines the size of the remnant population at the end of spraying.

4.1 The Survival of Original, Female Adults

How many of the original flies survive spraying? If a fly survives one spray cycle with probability ϕ , then the probability that it survives s consecutive sprays is ϕ^s , assuming the probability of survival for each spray is identical. The fly must also survive the normal hazards of life for the $(s - 1)\sigma$ days from the first through to the last spray. The maximum number of females from the original population which survive to the conclusion of spraying, is therefore

$$N e^{-\delta_2(s-1)\sigma} \phi^s, \quad (1)$$

in which N is the original, steady-state, equilibrium number of females prior to spraying and δ_2 is the worst-case-scenario, adult mortality rate.

A simplification made in this formula is that no age distribution profile has been assumed for the natural mortality. It should, however, be pointed out that, while the original proportion of females which have not yet ovulated is significant, the duration of the time preceding ovulation is insignificant when compared to the length of the spraying operation itself. The average

female fly, yet to ovulate, will also already be of an age greater than zero and the full time from eclosion to ovulation is therefore not under consideration, rather some fraction of it. A further fact to bear in mind is that, in the field, teneral are not attracted in the same proportions as adult flies when measuring the size of the original, equilibrium population. Of course, in the final analysis, the natural mortality used matters little as the spray-survival rate, ϕ , is a small number. The chances of any of the original flies surviving several spray cycles are usually practically zero.

4.2 The Survival of the Female Flies Which Eclosed from Original Pupae

How many flies initially eclosed from such pupae? Assuming a population which was in equilibrium at some mean temperature prior to the commencement of spraying, the daily number of flies eclosing from pre-spray-deposited pupae, is a constant

$$E_{\text{pre-spray}} = \beta N,$$

in which β is the steady-state eclosion rate previously described. Such flies continue to eclose for a period of one puparial duration subsequent to the commencement of spraying.

How many spray cycles will a given cohort be subjected to? The total number of spray cycles that a fly will be subjected to is determined by its day of eclosion, \check{t} . The time, during the operation, that it spent above ground is the length of the operation less the time before eclosion, that is $\sigma(s-1) - \check{t}$. The total number of insecticidal spraying cycles the fly will be subjected to is one more than the number of times a complete spray cycle fits into the period spent above ground. More succinctly,

$$\text{floor} \left\{ \frac{\sigma(s-1) - \check{t}}{\sigma} \right\} + 1,$$

where $\text{floor} \{ \cdot \}$ is the greatest integer function and \check{t} is the time from the first spray cycle to eclosion. The spray-survival rate, ϕ , must be applied this many times, so that the fraction of flies which survives the entire operation is

$$\phi^{\text{floor} \left\{ \frac{\sigma(s-1) - \check{t}}{\sigma} \right\} + 1}.$$

What of natural mortality? The flies die off naturally at some age-dependent mortality, $\delta^*(t - \check{t}, T)$.

What is the total number of flies of such origins remaining at the end of spraying? Collecting the above three observations, the number of female flies surviving at some later time, t , is

$$\gamma \sum_{\check{t}=1}^{\tau_0(T)} E_{\text{pre-spray}} e^{-\delta^*(t-\check{t}, T)} \phi^{\text{floor} \left\{ \frac{\sigma(s-1) - \check{t}}{\sigma} \right\} + 1}.$$

At the completion of the operation, the total time elapsed is $(s-1)\sigma$, and taking cognisance of the fact that the number of flies eclosing from pre-spray-deposited pupae must be constant for

a population which was in equilibrium at some mean temperature, prior to the commencement of spraying, yields

$$\gamma\beta N \sum_{\check{t}=1}^{\tau_0(T)} e^{-\delta^*((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1}. \quad (2)$$

What if the length of the operation is less than one puparial duration? In the event that the operation is curtailed to such an extent that the cycles are terminated before τ_0 , then not all the original pupae have the opportunity to eclose as flies and the remaining fraction contribute to the pupal population, still in the ground at the end of spraying. Under these circumstances, the above summation is truncated so that the upper limit, $\tau_0(T)$ is replaced with $\sigma(s-1)$. A further, extraordinary, pupal contribution must then also be added to the tally of pupae, still present in the ground at the end of spraying.

4.3 The Production and Survival of Female Flies from inter-spray Pupae

The last of the category “original pupae” eclose the moment one puparial duration since the commencement of spraying has elapsed. All the flies eclosing thereafter are of an inter-spray-larviposited origin. If, however, spraying is curtailed to the extent that its duration is less than one puparial duration, then none of this latter category ever eclose. Under such circumstances they exist solely as pupae, still in the ground at the end of spraying.

Otherwise, the survival of flies eclosing from inter-spray pupae can be deduced by similar reasoning to the aforementioned case, one difference being that the number of emergent flies is no longer constant over time (the eclosing population no longer being in equilibrium, or constant). Contributions to the time- \check{t} -eclosing cohort arise as a result of pupae which were larviposited $\check{t} - \tau_0$ days before. The number of such flies at the conclusion of spraying is

$$\gamma \sum_{\check{t}=\tau_0(T)+1}^{\sigma(s-1)} E(\check{t}) e^{-\delta^*((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1}. \quad (3)$$

The pupae were deposited by the previous, two survival categories and the inter-spray pupae, themselves. That is,

$$E(\check{t}) = E_a(\check{t}) + E_{ps}(\check{t}) + E_{is}(\check{t}),$$

in which the time- \check{t} -eclosing cohorts are defined in Table 1, according to their ancestral origins.

What of the ‘knock-down’ approach to the aerial spraying of tsetse? For instances in which the duration of an operation has been curtailed to the length of one puparial duration, or less, there is clearly no such contribution to flies, only pupae. Under such circumstances this second and higher generation category of flies may be completely disregarded. They need only be considered from the point of view of a pupal population.

4.3.1 The $E_a(\check{t})$ Contribution to $E(\check{t})$

This is the contribution attributed to larviposition by original, adult females, those which existed as such prior to the commencement of spraying and which larviposit during the operation. By far the largest mass of the pupae larviposited by original adults are larviposited during the first spray cycle, between the first and second sprays. Their eclosion commences immediately after the last of the pre-spray-larviposited pupae have emerged. They and a varying proportion of the pupae larviposited during the second cycle, eclose during the aerial spraying, for a completed operation. The majority of them are exposed to the last, or last two, sprays, for such a completed operation. Terminating the operation one spray short allows all the pupae larviposited in the second cycle and a varying proportion of those larviposited during the first cycle, never to be sprayed, in theory.

How many original mothers larviposit on a given day during the spraying? If there were N females prior to spraying, to assume that all have already ovulated is a worst-case scenario, therefore a safe assumption. Inseminated females, all ηN of them, are expected to deposit one pupa every τ_2 days; that is, the larviposition of $\frac{\eta N}{\tau_2}$ pupae every day.

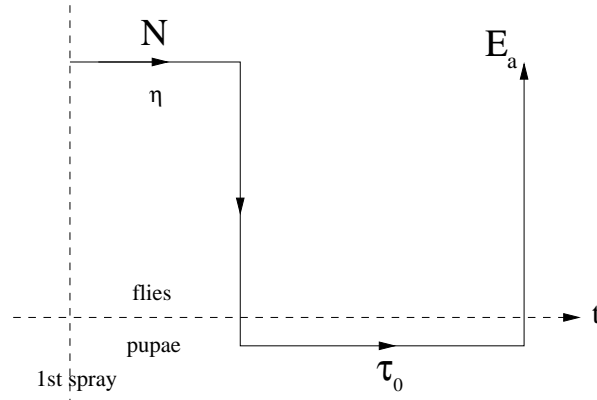


Figure 3: Schematic diagram of second generation flies eclosed from pupae that were larviposited during spraying by original, pre-spray-existing adults.

How many of these potential mothers survive until a given day into the spraying operation? The proportion of these adult mothers which survive naturally as long as $\check{t} - \tau_0$ into spraying is $e^{-\delta_2(\check{t}-\tau_0)}$ and they are, in turn, subjected to

$$\text{floor} \left\{ \frac{\check{t} - \tau_0 - 1}{\sigma} \right\} + 1$$

sprays (by contemplating Figure 3 and assuming larviposition is successfully accomplished shortly before spraying on the day in question). If a fly survives one spraying cycle with probability ϕ , then the probability that it survives the above number of cycles is

$$\phi^{\text{floor} \left\{ \frac{\check{t} - \tau_0 - 1}{\sigma} \right\} + 1},$$

always assuming the probability of survival for each cycle is identical.

How many of their daughters, in turn, survive to eclose? Taking natural mortality into account, the proportion of their pupae which survive to eclose is $e^{-\delta_0 \tau_0}$.

Hence, the final expression

$$E_a(\check{t}) = \eta \frac{N}{\tau_2} e^{-\delta_2(\check{t}-\tau_0)-\delta_0 \tau_0} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}+1} H(\check{t}-\tau_0), \quad (4)$$

in which H is the version of the Heaviside step function with $H(0) = 0$. One prerequisite for such E_a contributions to a second generation of flies is a restriction on the eclosion of the cohorts, $\check{t} > \tau_0$ (again, by contemplating Figure 3). Otherwise they need only be considered from the point of view of a pupal population.

4.3.2 The $E_{ps}(\check{t})$ Contribution to $E(\check{t})$

This is the contribution attributed to larviposition by mothers which existed as pupae at the commencement of spraying. Many such pupae eclose subsequent to the last spray, even for a completed operation. Under normal circumstances, this category may be thought of as the problem category. How many such mothers come into existence on a given day during the operation? The number of potential mothers, eclosing daily (for a limited period), from pre-spray-deposited pupae that will subsequently be inseminated, is

$$\gamma \eta E_{\text{pre-spray}} = \gamma \eta \beta N,$$

in which β is the steady-state, maximum possible, eclosion rate previously described, N is the original, steady-state, equilibrium number of females prior to spraying, γ is the probability of being female and η is the probability of insemination. Mothers of this category cease eclosing one puparial duration into the operation.

What is the subsequent mortality of these mothers? These pre-spray-larviposited mothers suffer a daily natural mortality of $\delta^*(\tau_1 + i\tau_2, T)$ and, by contemplating Figure 4, are subjected to a total of

$$\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\} - \text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}$$

sprays, this being the difference between the total number of sprays to larviposition and the total number of sprays up to the day before the mother's eclosion. If a fly survives one spraying cycle with probability ϕ , then the probability that it survives the above number of cycles is

$$\phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\} - \text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}},$$

always assuming the probability of survival for each cycle is identical and that larviposition will be successfully accomplished before spraying on relevant days. The survival of such mothers is therefore readily quantifiable in terms of the above.

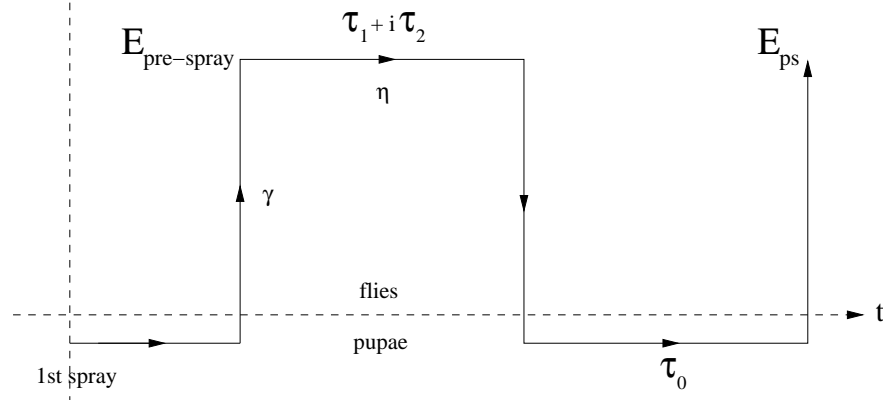


Figure 4: Schematic diagram of second generation flies ecloding from pupae that were larviposited by flies from original pupae that existed as such at the commencement of spraying.

What are the temporal restrictions on the eclosion of the second generation cohorts these mothers produce? By contemplating Figure 4, the first requirement for second-generation descent from such mothers, is a restriction on the cohorts to $\check{t} > \tau_0 + \tau_1$. The mothers would otherwise have had to have eclosed prior to the first spray, a fact which would exclude them from the category presently under consideration, altogether. Secondly, only for a limited period of time (one puparial duration) do mothers which originate from pre-spray-deposited pupae continue to emerge from the ground. That is, if all τ s are integer cohorts,

$$1 \leq \check{t} - \tau_0 - \tau_1 - i\tau_2 \leq \tau_0 \quad i = 0, 1, \dots,$$

yielding a restriction on i ,

$$i \leq \text{floor} \left\{ \frac{1}{\tau_2} (\check{t} - \tau_0 - \tau_1 - 1) \right\},$$

and completing those on the time of eclosion,

$$\tau_0 + \tau_1 + i\tau_2 < \check{t} \leq 2\tau_0 + \tau_1 + i\tau_2.$$

Lastly, only an $e^{-\delta_0 \tau_0}$ fraction of the pupae survive to eclode. Collecting all of the above information

$$E_{ps}(\check{t}) = \gamma\eta\beta N \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-\tau_0-\tau_1-1)\right\}} \left[e^{-\delta^*(\tau_1+i\tau_2,T)-\delta_0\tau_0} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} \right. \\ \left. [1 - H(\check{t} - 2\tau_0 - \tau_1 - i\tau_2)] H(\check{t} - \tau_0 - \tau_1 - i\tau_2) \right], \quad (5)$$

in which H is the version of the Heaviside step function with $H(0) = 0$. Notice that the last Heaviside factor becomes a precaution once i is greater than zero, since it is derived from the same inequality used for the restriction on i . Clearly there is no E_{ps} contribution to flies for instances in which the duration of the operation has been curtailed to, or below, the time between parturition and the production of the first larva, although pupae of this category will certainly exist.

Modifications for a Continuous Model

What if a continuous rather than discrete model were to be entertained? What if the τ s had not been rounded off to integer cohorts? What if they involved fractions of a day, instead? The i would, nonetheless, still be integers in such a model although, by analogous reasoning to that above,

$$0 < \check{t} - \tau_0 - \tau_1 - i\tau_2 < \tau_0 \quad i = 0, 1, \dots,$$

This would lead to a modification of the upper bound in the above summation, one based on

$$\max\{i\} < \frac{1}{\tau_2}(\check{t} - \tau_0 - \tau_1),$$

as well as the replacement of

$$[1 - H(\check{t} - 2\tau_0 - \tau_1 - i\tau_2)] \quad \text{with} \quad H(-\check{t} + 2\tau_0 + \tau_1 + i\tau_2).$$

The new switch differs in that it turns off when the argument zero, instead of immediately above it. So far as the number of sprays is concerned, ‘the-moment-before’ replaces the ‘the-day-before’ of the discrete case, so that the relevant factor becomes

$$\phi^{\text{floor}\left\{\frac{\check{t}-\tau_0}{\sigma}\right\} - \text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2}{\sigma}\right\}}.$$

4.3.3 The $E_{is}(\check{t})$ Contribution to $E(\check{t})$

This is the contribution attributed to female flies descended from the mothers which were themselves larviposited during spraying. They are the immediate descendants of the E_a category, the E_{ps} category, or this very same E_{is} category itself. The first prerequisite for such third, or greater, generation contributions is that $\check{t} > 2\tau_0 + \tau_1$ (by contemplating Figure 5).

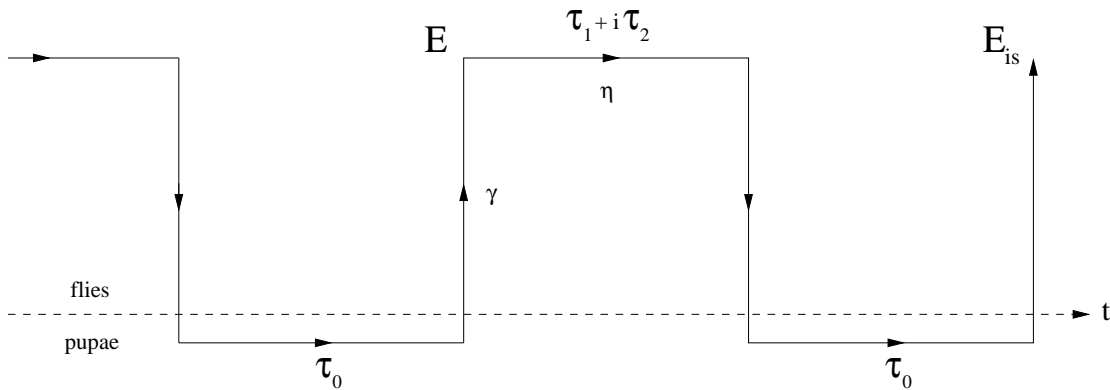


Figure 5: Schematic diagram of flies emerging from inter-spray pupae that are descended from inter-spray pupae themselves (third generation and higher).

Secondly, inter-spray-deposited pupal mothers only begin to eclode at time $\tau_0 + 1$, (just when the pre-spray pupae, have ceased to eclode). That is, if the various τ s are integer cohorts,

$$\tau_0 + 1 \leq \check{t} - \tau_0 - \tau_1 - i\tau_2 \quad i = 0, 1, \dots,$$

yielding a restriction on i ,

$$i \leq \text{floor} \left\{ \frac{1}{\tau_2} (\check{t} - 2\tau_0 - \tau_1 - 1) \right\}.$$

The probability that such mothers survive the relevant number of spray cycles is formulated in the same way as in the previous case; as is the natural mortality. The pupal mortality of the mothers and the mortality of the grandmothers is already taken care of by the E_a and E_{ps} categories. Taking cognizance of the fact that the emergent population is not constant over time under such circumstances,

$$E_{is}(\check{t}) = \gamma\eta \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-2\tau_0-\tau_1-1)\right\}} \left[E(\check{t} - \tau_0 - \tau_1 - i\tau_2) e^{-\delta^*(\tau_1+i\tau_2,T)-\delta_0\tau_0} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} H(\check{t} - 2\tau_0 - \tau_1 - i\tau_2) \right]. \quad (6)$$

Notice, once again, that the Heaviside factor becomes a precaution once i is greater than zero, since it is derived from the same inequality used for the restriction on i . There is no E_{is} contribution to flies for instances in which the duration of the operation is equal to, or below, the length of two puparial durations and the time to the first larva. In fact, normal circumstances make it difficult to imagine the category E_{is} as ever having eclosed by the end of spraying, therefore as having any relevance to the total fly tally at all. E_{is} may usually be neglected in the fly calculation. Neither is there any E_{is} contribution to pupae for instances in which the duration of the spray operation is equal to, or below, the length of time between parturition and the production of the first larva. E may, in practice and under normal circumstances, be assumed to have only two contributions, E_a and E_{ps} .

From this point on the origins of the inter-spray pupae are no longer relevant. Generations higher than the third are accounted for through recursion, in theory. In practice, the relative durations of the spraying operation, the puparial stage and the time between eclosion and the production of the first larva are such that it is difficult to imagine a scenario involving a fourth generation, consequently any recurrence relation at all.

Modifications for a Continuous Model

What if a continuous rather than discrete model were to be entertained? What if the τ s had not been rounded off to integer cohorts? What if they involve fractions of a day, instead? The i would still be an integer in such a model, however, by analogous reasoning to that above,

$$\tau_0 < \check{t} - \tau_0 - \tau_1 - i\tau_2 \quad i = 0, 1, \dots,$$

leading to a replacement of the upper bound in the above summation, one based on

$$\max\{i\} < \frac{1}{\tau_2}(\check{t} - 2\tau_0 - \tau_1).$$

So far as the number of sprays is concerned, ‘the-moment-before’ replaces the ‘the-day-before’ of the discrete case, so that the relevant factor becomes

$$\phi^{\text{floor}\left\{\frac{\check{t}-\tau_0}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2}{\sigma}\right\}},$$

as in the previous case.

5 Pupae Still in the Ground at the End of Spraying

The total number of female pupae, which are still in the ground at the end of spraying and **which will survive to eclose**, is the γ fraction of flies destined to begin eclosing as a series of cohorts immediately subsequent to the last spray. That is, starting at $\sigma(s-1) + 1$, and ending with $\sigma(s-1) + \tau_0$, in the discrete case. Contributions to this pupal population arise as a result of female pupae larviposited after the commencement of spraying, in a completed operation. They may be categorized as:

1. Daughters of original, female flies.
2. Daughters of original, female pupae.
3. Third generation and higher daughters of females which were larviposited after the commencement of the spraying.

A fourth contribution,

$$\gamma\beta N \sum_{\check{t}=\sigma(s-1)+1}^{\tau_0(T)} e^{-\delta^*((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1} H(\tau_0 - (s-1)\sigma),$$

that due to the pressence of original pupae, must also be taken into account in an operation which has been curtailed to the extent that its duration is less than one puparial duration.

Otherwise, the total number of such female pupae remaining in the ground at the end of spraying and **which will survive to eclose**, is

$$\gamma \sum_{\check{t}=\sigma(s-1)+1}^{\sigma(s-1)+\tau_0(T)} [E_a(\check{t}) + E_{ps}(\check{t}) + E_{is}(\check{t})]. \quad (7)$$

As it transpires, one of the above categories is far and away more important than any of the others in a completed operation. The pre-eminent category is the second one above, the pupae

which are destined to give rise to an E_{ps} eclosion after spraying. The implications of this discovery are that, under certain conditions, one formula can be adapted to provide a good estimate of the outcome of aerial spraying. This fact is revealed when considering that there is only one $O(\phi)$ contribution and this observation is further corroborated by the algorithm of Childs (2011). A compositional analysis of the origins of female pupae, still in the ground, reveals that summation of the second term in the above summation formula is a good indicator of the entire outcome of spraying, given a kill rate of 99.9%, or better. It accounts for well over 90% of the pupal population at a kill rate of 99%.

6 An Example of a Manual Calculation

At 24 °C, four sprays which define three spray cycles, of length 14 days each, are required. The aerial spraying scenario at this temperature is slightly simplified and lends itself favourably to manual calculation for two reasons. The first is that the time to the second last spray is, for all practical purposes, exactly one puparial duration. All the pupae deposited during the first spray cycle therefore eclose during the last spray cycle and the pupae still in the ground at the end of the operation were deposited during the second and third spray cycles. The second reason is that the spray operation ends early from a metabolic point of view, meaning that a third generation never exists during spraying, as is so often the case. For the aforementioned reasons any problems with the formulae should be relatively easy to detect.

Surviving Flies

Although the number of spray cycles is relatively small, the number of original adults which survive is still insignificant, it being of $O(\phi^4)$. Eq. 1 can accordingly be dismissed as negligible. This is usually the case in a completed operation. Those pre-spray-deposited pupae which eclose for the duration of the second cycle must survive only the last two sprays, instead of three, and Eq. 2 therefore becomes

$$\gamma\beta N \sum_{\check{t}=15}^{28} e^{-\delta^*(42-\check{t},24)} \phi^{\text{floor}\{\frac{42-\check{t}}{14}\}+1} + O(\phi^3).$$

The only categories left to consider are the second and third generations, calculated according to Eq. 3. Both the E_{is} and E_{ps} terms can be dismissed as irrelevant to the fly population, since the length of the operation is shorter than the time from parturition to the production of the first larva. Relevant second generation flies are therefore all descended from the original, pre-spray-existing flies, those which survived the first spray. This E_a contribution is also a significant, $O(\phi^2)$ contribution, since the pupae were deposited during the first spray cycle and eclose for the duration of the last spray cycle. Eq. 3 therefore becomes

$$\gamma \sum_{\check{t}=29}^{42} \eta \frac{N}{10} e^{-0.024(\check{t}-28)-0.01 \cdot 28} \phi^{\text{floor}\{\frac{\check{t}-28-1}{14}\}+1} \cdot 1 \cdot e^{-\delta^*(42-\check{t},24)} \phi^{\text{floor}\{\frac{42-\check{t}}{14}\}+1} + O(\phi^3).$$

If one very crudely approximates $e^{-\delta^*(42-\check{t},24)}$ as 0.5231, $e^{-0.024(\check{t}-28)-0.01\cdot 28}$ as 0.6389 and $e^{-\delta^*(42-\check{t},24)}$ as 0.7320, in a ‘back-of-an-envelope’ fashion and based on the relevant Childs (2011) mortalities, the sum of the preceding two expressions becomes

$$14 \times 0.5 \times N \left(0.0466 \times 0.5231 + 1 \times \frac{1}{10} \times 0.6389 \times 0.7320 \right) \phi^2 + O(\phi^3),$$

using a β of 0.0466.

Surviving Pupae

Only Eq. 7 is relevant to the pupal outcome, since the operation is not shorter than one puparial duration. The E_{is} contribution can be dismissed as irrelevant, since the length of the spray operation is shorter than $\tau_0 + \tau_1$. In order for pupae to contribute to an E_a eclosion subsequent to the completion of the operation, they must have been larviposited in the second or third cycles (those which were larviposited in the first cycle have already eclosed by the end of spraying). This means that their mothers were sprayed at least twice and accordingly they constitute an $O(\phi^2)$ contribution. There is only one significant, $O(\phi)$ contribution to the pupal population; that destined to give rise to an E_{ps} eclosion. The pupal outcome can therefore be crudely formulated in terms of Eq. 7 as

$$\eta \gamma^2 N \beta \sum_{\check{t}=43}^{70} \sum_{i=0}^{\text{floor}\left\{\frac{1}{10}(\check{t}-28-16-1)\right\}} \left[e^{-\delta(28+16+i10,24)} \phi^{\text{floor}\left\{\frac{\check{t}-28-1}{14}\right\} - \text{floor}\left\{\frac{\check{t}-28-16-i10-1}{14}\right\}} \right. \\ \left. [1 - H(\check{t} - 56 - 16 - i10)] H(\check{t} - 28 - 16 - i10) \right] + O(\phi^2).$$

This contribution arises as a result of mothers which eclose from original pupae during the first and second cycles and which subsequently survive a single spray to larviposit in the second and third cycles. Examination of the above formula reveals significant, $O(\phi)$ terms only for the combinations of i and \check{t} represented in

$$1 \times 0.25 \times N \times 0.0466 \left[\sum_{\check{t}=45}^{56} e^{-\delta(44,24)} + \sum_{\check{t}=59}^{70} e^{-\delta(44,24)} \right. \\ \left. + \sum_{\check{t}=55}^{56} e^{-\delta(44+10,24)} + \sum_{\check{t}=69}^{70} e^{-\delta(44+10,24)} \right] \phi + O(\phi^2).$$

Results

Assuming the same mortalities and the same 8 000 000, original, steady-state number of females as in Childs (2011), the estimated outcome for surviving, female pupae and flies is as presented in Table 2.

ϕ	flies	$\log(\text{flies})$	pupae	$\log(\text{pupae})$
0.01	398	2.60	12098	4.08
0.001	4	0.60	1210	3.08
0.0001	0	-	121	2.08

Table 2: Estimated female survival for the simple case of 24 °C, based on low order terms.

The results only differ from those of the Childs (2011) algorithm insofar as a more cautious choice of β has been made.

7 Conclusions

Repeated spray cycles are scheduled at intervals two days short of the time between eclosion and the production of the first larva,

$$\sigma = \frac{1}{0.061 + 0.0020 (T - 24)} - 2,$$

and, in a completed operation, continue until two sprays subsequent to the eclosion of the last, pre-spray-deposited, female pupae. That is,

$$s = \text{ceil} \left\{ \frac{1 + e^{5.5 - 0.25T}}{0.057 \sigma} \right\} + 2,$$

in which $\text{ceil} \{.\}$ is the least integer function.

Spray efficacy is found to come at a price due to the greater number of cycles necessitated by cooler weather. The greater number of cycles is a consequence of a larger ratio of puparial duration to time-to-first-larva at lower temperatures. The prospect of a more expensive spraying operation at low temperature, due to a greater, requisite number of spray cycles is, however, one which is never confronted in the real world. In reality, one has to strive towards kill rates and the only way such rates can be attained is by spraying at as low a temperature as possible (Hargrove, 2009).

A refinement of the existing formulae for the puparial duration and the time between eclosion and the production of the first larva might be prudent in the South African context of a sympatric *G. brevipalpis*-*G. austeni*, tsetse population.

7.1 The Complete Set of Formulae

The complete set of formulae derived for the performance of a tsetse population under conditions of aerial spraying is summarised as follows.

Pupae

The following are the contributions to female pupae, still in the ground at the end of spraying, **which will survive to eclose**. The number of such pupae which are daughters of original adults is

$$\eta\gamma\frac{N}{\tau_2}\sum_{\check{t}=\sigma(s-1)+1}^{\sigma(s-1)+\tau_0} e^{-\delta_2(\check{t}-\tau_0)-\delta_0\tau_0}\phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}+1} H(\check{t}-\tau_0). \quad (8)$$

The number of pupae which are daughters of original pupae is

$$\eta\gamma^2 N\beta\sum_{\check{t}=\sigma(s-1)+1}^{\sigma(s-1)+\tau_0} \sum_{i=0}^{\text{rmfloor}\left\{\frac{1}{\tau_2}(\check{t}-\tau_0-\tau_1-1)\right\}} \left[e^{-\delta(\tau_0+\tau_1+i\tau_2,T)} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} \right. \\ \left. [1 - H(\check{t}-2\tau_0-\tau_1-i\tau_2)] H(\check{t}-\tau_0-\tau_1-i\tau_2) \right]. \quad (9)$$

The number of pupae which are daughters of inter-spray pupae is

$$\eta\gamma^2\sum_{\check{t}=\sigma(s-1)+1}^{\sigma(s-1)+\tau_0} \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-2\tau_0-\tau_1-1)\right\}} \left[E(\check{t}-\tau_0-\tau_1-i\tau_2) e^{-\delta(\tau_0+\tau_1+i\tau_2,T)} \right. \\ \left. \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} H(\check{t}-2\tau_0-\tau_1-i\tau_2) \right]. \quad (10)$$

If the aerial spraying operation is curtailed to the extent that it is shorter than one puparial duration, then an additional category of pupae must be accounted for. The number of original pupae, those larviposited before the commencement of spraying, which have not yet eclosed by the end of spraying, is

$$\gamma\beta N\sum_{\check{t}=\sigma(s-1)+1}^{\tau_0(T)} e^{-\delta^*((s-1)\sigma-\check{t},T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1} H(\tau_0-(s-1)\sigma). \quad (11)$$

Flies

The following are the contributions to female flies which survive to the conclusion of spraying. The maximum number of such surviving, female flies from the original population, is

$$N e^{-\delta_2(T)(s-1)\sigma}\phi^s. \quad (12)$$

The number of surviving female flies which eclosed during spraying from original pupae is

$$\gamma\beta N \sum_{\check{t}=1}^{\min\{\tau_0(T), \sigma(s-1)\}} e^{-\delta^*((s-1)\sigma-\check{t}, T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1}. \quad (13)$$

The number of surviving female flies that eclosed from inter-spray-larviposited pupae and which will survive until after the last spray is

$$\gamma \sum_{\check{t}=\tau_0(T)+1}^{\sigma(s-1)} [E_a(\check{t}) + E_{ps}(\check{t}) + E_{is}(\check{t})] e^{-\delta^*((s-1)\sigma-\check{t}, T)} \phi^{\text{floor}\left\{\frac{\sigma(s-1)-\check{t}}{\sigma}\right\}+1}, \quad (14)$$

in which the respective time- \check{t} -eclosing cohorts are given by

$$\begin{aligned} E_a(\check{t}) &= \eta \frac{N}{\tau_2} e^{-\delta_2(\check{t}-\tau_0)-\delta_0\tau_0} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}+1} H(\check{t} - \tau_0), \\ E_{ps}(\check{t}) &= \gamma\eta\beta N \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-\tau_0-\tau_1-1)\right\}} \left[e^{-\delta(\tau_0+\tau_1+i\tau_2, T)} \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} \right. \\ &\quad \left. [1 - H(\check{t} - 2\tau_0 - \tau_1 - i\tau_2)] H(\check{t} - \tau_0 - \tau_1 - i\tau_2) \right], \\ E_{is}(\check{t}) &= \gamma\eta \sum_{i=0}^{\text{floor}\left\{\frac{1}{\tau_2}(\check{t}-2\tau_0-\tau_1-1)\right\}} \left[E(\check{t} - \tau_0 - \tau_1 - i\tau_2) e^{-\delta(\tau_0+\tau_1+i\tau_2, T)} \right. \\ &\quad \left. \phi^{\text{floor}\left\{\frac{\check{t}-\tau_0-1}{\sigma}\right\}-\text{floor}\left\{\frac{\check{t}-\tau_0-\tau_1-i\tau_2-1}{\sigma}\right\}} H(\check{t} - 2\tau_0 - \tau_1 - i\tau_2) \right]. \end{aligned}$$

Modifications for a Continuous Model

Minor modifications, listed at the ends of Subsections 4.3.2 and 4.3.3, need to be made if the discrete formulae are to be adapted to the continuous case. The summations over the cohorts $\sum_{\check{t}=1}^{\dots}$, $\sum_{\check{t}=\tau_0(T)+1}^{\dots}$ and $\sum_{\check{t}=\sigma(s-1)+1}^{\dots}$ would also be replaced with the integrals \int_0^{\dots} , $\int_{\tau_0(T)}^{\dots}$ and $\int_{\sigma(s-1)}^{\dots}$, respectively and among other things.

7.2 Which Formulae are Significant, Which are Insignificant and Which are Irrelevant?

The pupae which give rise to the E_{is} eclosion have, at best, hardly come into existence, let alone eclosed, by the end of a completed operation. The E_{is} contribution may therefore usually be regarded as irrelevant insofar as flies are concerned, whereas its contribution to the total pupal tally is usually insignificant, at most. The category E_{is} can be omitted from the Eq. 14 fly formula for all reasonable circumstances, that is, unless the operation has been greatly

extended. Clearly, there is no E_{is} contribution to the Eq. 14 fly formula for instances in which the duration of the operation is $2\tau_0 + \tau_1$, or less. There is also no Eq. 10 contribution involved in the pupal tally for instances in which the duration of the operation is $\tau_0 + \tau_1$, or less. Although this varies from case to case, the Eq. 10 contribution is never significant unless the operation has been greatly extended. The E_{ps} term can be omitted from the Eq. 14 fly formula for instances in which the duration of the operation is $\tau_0 + \tau_1$, or less. Take heed, however, that pupae, destined to give rise to a future E_{ps} eclosion (Eq. 9), are usually the most significant contribution, by far, in a completed operation. The only circumstances for which these pupae are irrelevant is for instances in which the duration of the operation involves a single cycle; that is, two sprays only. The category E_a can be omitted from the Eq. 14 fly formula for instances in which the duration of the operation is τ_0 , or less. The Eq. 8 pupae, those destined to give rise to just such an E_a eclosion, can never be irrelevant, since the larviposition of such pupae commences immediately after the first spray. A lengthly spray operation can, however, still render their contribution insignificant, since such mothers become progressively decimated and the earlier pupal mass will eclose before the operation is complete. Generally, the more curtailed the spraying operation, the fewer contributing categories there are, with one exception: In the event that an operation is curtailed to the extent that its duration is less than one puparial duration, a proportion of the original pupae remain in the ground at the end of spraying. This complicates matters slightly. Under such circumstances the series of flies, Eq. 2, is truncated as specified in the formula Eq. 13, the remainder being additional pupae which will survive, as quantified by Eq. 11. These same circumstances render the entire Eq. 14 fly formula irrelevant.

In a completed operation, by far the most significant category is that calculated in terms of Eq. 9 above. These are pupae which are destined to give rise to an E_{ps} eclosion once the operation is complete. The magnitude of this contribution is easy to see when one considers that many of their mothers (original pupae which eclose during spraying) will only be sprayed once (see Fig. 4). Since all pupae are, by definition, never sprayed if they are still in the ground at the end of spraying, the E_{ps} lineage constitutes an $O(\phi)$ contribution to pupae. In contrast, the mothers of pupae destined to give rise to an E_a eclosion, after spraying, must be sprayed more than once if these daughters are still to be pupae by the end of the operation. Otherwise, they would already have eclosed (see Fig. 3). The Eq. 8 lineage may therefore be regarded as being of $O(\phi^2)$ significance. The Eq. 10 lineage (pupae destined to give rise to an E_{is} eclosion, after spraying) also constitutes an $O(\phi^2)$ contribution (see Fig. 5). A large number of the pupae destined to give rise to an E_{ps} eclosion will therefore always be of a lower order than those destined to give rise to an E_a or an E_{is} eclosion, in a completed operation. Notice that all lineages which exist as flies at the time of the last spray will be of order $O(\phi^2)$, or higher, in a completed operation. This is easy to see when one considers that all these flies must, by definition, be subjected to the last spray. The length of a complete operation means that their lineage must also have been sprayed at least once during the operation. That the daughters of the original pupae, Eq. 9, are a good forecast of the outcome of a completed operation, given a kill rate of 99.9% or better, is further corroborated by the algorithm of Childs (2011).

Given the high kill rates attainable, it is not surprising that the outcome, for flies (as distinct from pupae), is largely determined by the size of the emergent population which was only subjected to the last two sprays, in a completed operation. This is why the proportion of

flies was relatively high in the Section 6 example. A full cycle's worth of original pupae eclosed to be followed by a full cycle's worth of E_a eclosion during the last two cycles of that example. The actual flies, themselves, which survive the last spray of a completed operation are, however, of no real consequence to the outcome. Under such circumstances, pupae, still in the ground at the end of spraying, are identified as the main threat to successful control by aerial spraying. The outcome, for kill rates of 99.9%, or higher, was shown in Childs (2011) to be almost exclusively dependent on the immediate descendants of the original pupae, those pupae which were present at the commencement of spraying. Even at kill rates as low as 99% this Eq. 9 category still constitutes around 90% of the surviving female population in a completed operation while the Eq. 8 contribution accounts for less than 10% of the total pupal population (Childs, 2011).

If, however, operations are halted one or more sprays short, these generalisations can not be made. Not only is the recently-eclosed fly population still significant, there is also a fairly large pupal population descended from the original adults. The contribution of the Eq. 8 category and others, becomes significant. The total predominance of Eq. 9 does not exist. Some of the pupae destined to give rise to an E_a eclosion become a significant, $O(\phi)$ contribution, as do some of the flies that eclosed from original pupae. While flies arising from the E_a eclosion, itself, are only of order $O(\phi^2)$, it should also be remembered that they were larviposited during the first cycle, when the population of original, adult flies was still strong. The formulae Eq. 8, Eq. 9, Eq. 12, Eq. 13 and part of Eq. 14 all need to be considered if the operation is halted one spray short. The Eq. 9 contribution is always significant and that of Eq. 12 insignificant. Only the E_a term in Eq. 14 is still relevant under such circumstances. If the last spray falls close to a full cycle's length from the one-puparial-duration mark, then the Eq. 13 flies will be less significant, despite the fact that they are an $O(\phi)$ contribution, and one will find almost a cycles worth of $O(\phi^2)$, E_a eclosion (Eq. 14). If, on the other hand, the last spray falls close to the one-puparial-duration mark, then one will find almost a cycles worth of $O(\phi)$, Eq. 13 eclosion and the entire Eq. 14 contribution can be dismissed as insignificant. They will mostly still be in the ground as Eq. 8 pupae. Of course, a proportion of the alleged pupae might also actually be aging flies, under such circumstances, given the mechanism whereby mature, gravid females excrete lipophilic toxins to sacrifice larvae in utero for their own survival.

If the operation is halted two, or more, sprays short, the Eq. 14 fly formula falls away entirely while an Eq. 11 contribution comes into existence. Under these circumstances, only the formulae Eq. 8, Eq. 9, Eq. 11, Eq. 12 and Eq. 13 are relevant. The significance of the Eq. 11 contribution will be proportional to the time between the last spray and the one-puparial-duration mark. Of course, the original, surviving adults (Eq. 12) can almost always be regarded as insignificant, they being an $O(\phi^s)$ contribution. That is, for all except the most severely curtailed operation.

7.3 Factors Extraneous to a Theoretical Outcome

It is important to remember that the formulae calculate a theoretical outcome based on the premise that no practical problems will be encountered in the field. The idea of this work has

been to create a simple arithmetic tool which can be used to establish conditions sufficient for a successful operation in the context of a closed tsetse population. Hargrove (2005) quantifies the dangers in allowing the smallest of founding populations to survive and re-invasion is an ever present threat which will ultimately compromise even the most successful aerial spraying operation. A cursory inspection of the Rogers and Robinson (2004) study (based on the Ford and Katondo, 1977, maps) suggests that most tsetse populations cannot be considered closed. The total extent of habitat is a further cause for concern. Even the extant, forest-dwelling, tsetse populations of South Africa cannot be considered closed and extend beyond its borders (Hendrickx, 2007). By far the biggest threat to any aerial spraying operation on mainland Africa is re-invasion from adjacent, untreated areas. Closed populations need to be created by temporary barriers of odour-baited targets such as the one used successfully by Kgori et al., 2006. Childs (2010) and Esterhuizen et al. (2006) comprehensively researched the design of such odour-baited, target barriers for *G. austeni* and *G. brevipalpis*; albeit mostly from a point of view of a control in its own right. In Childs (2011), the same model was re-run with a more stringent, *G. austeni* isolation standard than that used for control in Childs, 2010.

Quantifying spray efficacy represents a further problem. Temperature doesn't only effect the aerial spraying of tsetse, through its reproductive cycle and general population dynamics. Cooler weather is preferred for aerial spraying from a point of view of spray efficacy (Hargrove, 2009). Very high kill rates usually (though not always) come about as a result of the sinking air associated with cooler weather. It favours the settling of insecticidal droplets. Although Du Toit (1954) makes mention of the sustained down draught from a slow-moving helicopter, there are obviously distinct disadvantages to such a method of insecticide application. The inherent toxicity of deltamethrin and many other pyrethroids also decreases with temperature, contrary to the toxicity of most insecticides. The effects of temperature on spray efficacy are not modelled. For that matter, neither are the effects of anabatic winds, nor the protection afforded by the forest canopy and multifarious other variables relevant to spray efficacy. Spray efficacy is usually measured in the field, with hindsight, rather than predicted.

It has been assumed that gravid female resistance to the insecticide can be ignored. Although it may be tempting to consider the model poorer for this lack of detail, it may not be a deficiency of any consequence, since a simple trade-off exists between a fly living and a larva dying. Further pregnancies during the operation should, similarly, terminate in spontaneous abortion. Another point to bear in mind is that the spray-survival rate is a small fraction. Whatever the exact value of ϕ may be for the older flies, the value of ϕ^s , or similar, should ordinarily ensure that they have been decimated. Gravid female resistance is sure to result in the use of slightly altered eclosion rates and inappropriate natural mortalities, however, some comfort can be taken from the knowledge that the effects of natural mortalities are very small in comparison to those due to aerial spraying. They have little bearing on the outcome.

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